JM
Journal of Mammalogy, 91(1):79–91, 2010

Diet and food availability: implications for foraging and dispersal of Prince of Wales northern flying squirrels across managed landscapes

Elizabeth A. Flaherty,* Merav Ben-David, and Winston P. Smith

Department of Zoology and Physiology, University of Wyoming, Department 3166, 1000 E University Avenue, Laramie, WY 82070, USA (EAF, MB-D)
United States Department of Agriculture Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA (WPS)

* *Correspondent: lizf@uwyo.edu*

Where dispersal is energetically expensive, feeding and food availability can influence dispersal success. The endemic Prince of Wales northern flying squirrel (*Glaucomys sabrinus griseifrons*) inhabits a landscape mosaic of old-growth, 2nd-growth, and clear-cut stands, with the latter 2 representing energetically expensive habitats. We estimated the diet of flying squirrels using stable isotope and fecal analyses, determined whether food availability varies among forest stands, and assessed the likelihood of foraging across a managed landscape given the distribution of foods on Prince of Wales Island (POW), Alaska. Both stable isotope and fecal analyses revealed that conifer seeds, lichens, and fungi were the main dietary items consumed and assimilated by flying squirrels. Similarly, soil macroinvertebrates were consumed by squirrels, whereas berries were not. Nonetheless, although examination of stable isotope data suggested that squirrels assimilated few nutrients from truffles, this food source was among the most frequent diet items in feces, probably because flying squirrels assimilate elements other than nitrogen from fungi. Our surveys showed that conifer seeds, truffles, and lichens were more prevalent in old-growth than 2nd-growth and clear-cut habitats. Thus, our results indicate that diet and availability of food items on POW may influence foraging success and dispersal movements of *G. sabrinus* across fragmented landscapes because of limited availability of food resources in the managed habitats. DOI: 10.1644/09-MAMM-A-014R.1.

Key words: clear-cuts, fecal analyses, fungi, old-growth forests, soil macroinvertebrates, Southeast Alaska, stable isotope analysis, truffles

The endemic Prince of Wales flying squirrel (*Glaucomys sabrinus griseifrons* Howell, 1934) inhabits a habitat altered significantly by broadscale timber harvest; the once near contiguous old-growth Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) forests are now a mosaic of old-growth remnants, younger 2nd-growth stands (<60 years in age), and clear-cuts. Future timber harvest will further fragment the old-growth forest on Prince of Wales Island (POW), Alaska. Current plans to maintain a system of old-growth reserves assume that, despite the increased fragmentation, populations of old-growth obligate species will function as metapopulations through continued dispersal among old-growth isolates (United States Department of Agriculture Forest Service 1997). However, our recent studies demonstrated that flying squirrels gliding into 2nd-growth and clear-cut habitats may experience difficulties orienting toward the nearest forest edge, especially on cloudy, rainy nights (Flaherty et al. 2008). Under such conditions, which are common on POW, travel paths (relative to straight-line distance) of flying squirrels across clear-cut and 2nd-growth stands are considerably longer than in old-growth forests and are characterized by multiple pauses, which translate to greater travel time (Flaherty et al. 2008). In addition, we found that the cost of quadrupedal locomotion, the mode of transport adopted by squirrels in clear-cut and 2nd-growth stands, is higher than expected, especially when compared to other arboreal sciurids (E. A. Flaherty, pers. obs.). Thus, unless flying squirrels are able to replenish their depleted energy stores when dispersing across high-cost managed stands, successful dispersal and viable metapopulations are unlikely (Smith and Person 2007; Smith et al., in press).

Although the diet of *G. sabrinus* has been studied extensively (Smith 2007), limited information exists on the diet of populations in the temperate rain forests of Southeast Alaska (Pyare et al. 2002). Based on the diversity of spores identified in fecal samples in past studies, *G. sabrinus* appears to be primarily a mycophagist, specializing on the fruiting bodies of hypogeous mycorrhizal fungi (hereafter, truffles) in most parts of its range (Currah et al. 2000; Maser et al. 1986; Pyare et al. 2002). However, the reliance of *G. s. griseifrons* on fungi in Southeast Alaska may be lower than elsewhere (Pyare et al. 2002). Truffles have low nutritional value (Claridge et al. 1999; Cork and Kenagy 1989; Dubay et al. 2008), and by consuming a diversity of genera that differ in nutritional contents, squirrels are able to obtain essential nutrients (Claridge et al. 1999; Dubay et al. 2008). Because species diversity of truffles is lower in Southeast Alaska, flying squirrels may be unable to meet their nutritional needs by concentrating on truffles as a food source (Pyare et al. 2002). *G. sabrinus* augments its diet by consuming epigeous fungi (mushrooms); arboreal lichens such as *Bryoria*, *Usnea,* and *Alectoria* spp. (Maser et al. 1985; Rosentreter et al. 1997); berries; conifer seeds; new growth tips and buds from trees; bird eggs and young; animal tissue; and invertebrates (Maser et al. 1985; Thysell et al. 1997; Wells-Gosling and Heaney 1984).

Timber harvest changes the structure and microclimate of old-growth forests (Colgan 1997), removes the energy sources (trees) for fungi (Amaranthus et al. 1994; Colgan 1997), and damages the hyphal mat during logging operations (Carey et al. 2002). Thus, resulting clear-cuts, 2nd-growth, and thinned stands exhibit significantly lower fungal biomass and diversity than old-growth stands (Amaranthus et al. 1994; Carey et al. 2002; Waters et al. 1994), and little is known about the length of time required before fungi will reestablish colonies and begin to produce truffles (Amaranthus et al. 1994). The effects of timber harvest on the availability of other potential diet items of flying squirrels are even more obscure. Nonetheless, these managed habitats may be depleted not only in the preferred diet item, fungal fruiting bodies, but also in alternative foods. Such lower availability of food items may reduce the ability of dispersing flying squirrels to replenish their energy stores. Therefore, the objectives of our study were to estimate the relative importance of fungal fruiting bodies and other potential food items in the diet of northern flying squirrels in Southeast Alaska, determine if the abundance of those diet items varies between old-growth and managed forests, and evaluate whether dispersers would be expected to encounter adequate food resources while traversing managed landscapes of Southeast Alaska.

Materials and Methods

Study area.—Study sites were located on northern POW, Alaska, near the community of Naukati (55°52′N, 133°12′W; Fig. 1). The old-growth habitat is composed of Sitka spruce and western hemlock, with yellow cedar (*Xanthocyparis nootkatensis*) and western red cedar (*Thuja plicata*) occurring in more mesic areas. These old-growth stands contain many down, decaying logs and snags. The understory includes devil's club (*Oplopanax horridus*) and dense areas of *Vaccinium* spp. The 2nd-growth habitat is primarily ''dog-hair'' stands of spruce and hemlock (i.e., densely stocked with small-diameter trees that were on average no more than one-half the diameter of trees in old-growth—Alaback 1982). Second-growth rain forest in Southeast Alaska correspond ecologically to substantially younger 2nd-growth forests at lower latitudes because succession proceeds much slower (≥300 years to develop old-growth forest structure). The remainder of the study area was composed of clear-cuts, which are recently (<5 years) disturbed stands with no overstory and a vegetation layer that includes skunk cabbage (*Lysichitum americanum*) and *Vaccinium* spp., with some small pools of standing water.

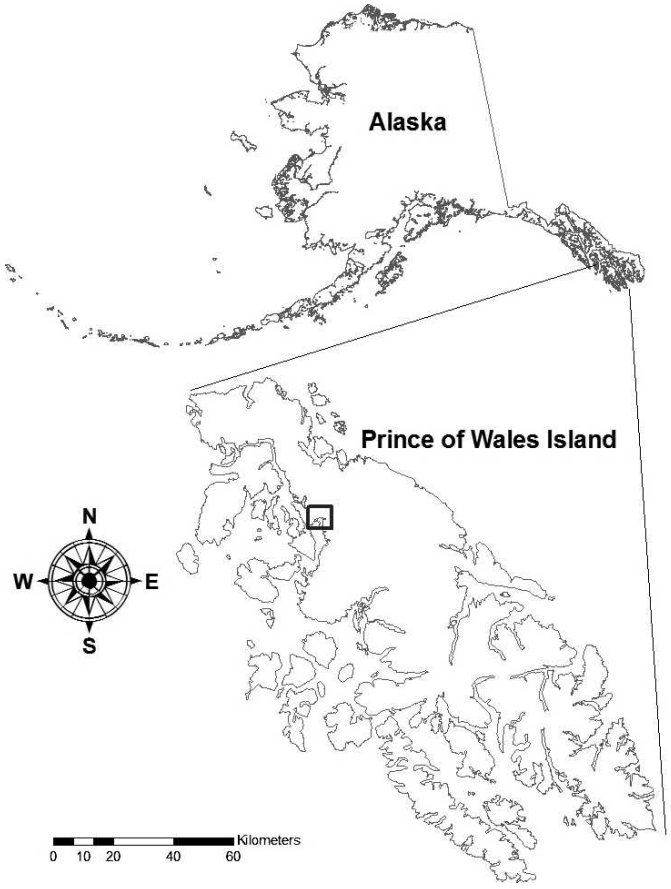

Fig. 1.—Map of core study area on Prince of Wales Island, Southeast Alaska. Trapping area was located inside the box. Surveys of food availability and trapping of northern flying squirrels (*Glaucomys sabrinus griseifrons*) occurred during spring 2003, 2004, and 2005, and autumn 2004 and 2005.

Livetrapping and sample collection.—Flying squirrels were trapped in the autumn months (August–October) of 2003–2005, a period that overlapped with juvenile dispersal, and the spring months (March–April) of 2004–2005, which corresponded with breeding dispersal. Trapping occurred on 3 different grids situated in old-growth forest stands within an

area of approximately 10 km^2. Because radiotelemetry, fine-scale movement, and perceptual range data all indicated that flying squirrels were avoiding clear-cut and 2nd-growth habitats (Flaherty et al. 2008; S. Pyare and W. P. Smith, per. obs.), and because Smith and Person (2007) determined that low-quality old-growth habitats (i.e., peatland–mixed conifer stands) act as population sinks on POW, we did not establish trapping grids in managed stands. Tomahawk No. 201 (13 × 13 × 41-cm) live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) were placed approximately 1.5 m above the forest floor on the bole of a tree and baited with a mixture of rolled oats, peanut butter, and molasses (Smith and Nichols 2003). Traps were checked at sunrise, and animals captured for the 1st time were marked with a unique passive integrated transponder tag (Biomark, Boise, Idaho); all captured individuals were weighed and sexed. We collected whole blood samples from each new captured adult for stable isotope analysis. Animals were briefly exposed to halothane, an inhalant anesthetic with a rapid induction rate and recovery (McColl and Boonstra 1999; Menzel et al. 2004), and we collected a small, triangular ear clipping from the medial edge of the right ear using a pair of sharp tissue scissors. We used microcapillary tubes to collect whole blood droplets from the ear. The tubes were stored inside sterile Whirlpacks (Nasco, Fort Atkinson, Wisconsin) and frozen. We collected blood samples only from adults because of the increased risk of mortality from cardiovascular depression associated with halothane exposure (McColl and Boonstra 1999) that could be exacerbated by the physiological stress from dispersal activity in juveniles. We also collected fecal pellets from the anus or from a clean, uncontaminated surface where they fell during handling (Carey et al. 2002; Lehmkuhl et al. 2004; Pyare et al. 2002). We excluded pellets that visibly included bait. Feces were stored in Whirlpacks and frozen. Field methods were approved by the University of Wyoming Institutional Animal Care and Use Committee and followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Estimating diet with stable isotope and fecal analyses.—We estimated the diet of flying squirrels using both stable isotope and fecal analyses. Stable isotope analysis determines the relative contribution of assimilated diet items, whereas fecal analysis yields information on the diversity of recently digested food (Angerbjörn et al. 1994), in this case fungi, through the identification of cells and spores. Stable isotope analysis provides an index of the relative contribution of each item in the diet (Ben-David and Schell 2001; Phillips and Koch 2002) through measurement of isotopic values of the heavy isotopes of carbon (C) and nitrogen (N) in the tissue of an animal and those in the potential diet items. In this analysis it is important to account for the difference between the isotopic values of the consumer and its diet, or diet-consumer discrimination, which stems from chemical or physiological processes (Gannes et al. 1997). In addition, for reliable estimates of diet contribution, all diet items should have distinctive isotopic signatures, and the appropriate tissues must be used because tissues differ in turnover rates, diet–consumer discrimination, and assimilation of different diet components (Gannes et al. 1997). For example, isotopic values of blood serum correspond with diet during a relatively short period of time, 1–2 weeks prior to sampling, whereas red blood cells reflect diet during the previous 2–3 months (Hilderbrand et al. 1996; Hobson and Clark 1993). Additionally, isotopic discrimination and routing of the different components from each food source (i.e., carbohydrates, lipids, and proteins) to consumer body tissues can complicate the interpretation of isotopic signatures (Gannes et al. 1998). However, the use of stable isotope analysis in conjunction with fecal analyses should provide more reliable estimates of diet composition because fecal analysis may underestimate use of some diet items and thus may not sufficiently describe the importance of some foods (Thysell et al. 1997). Furthermore, unless fecal samples are assigned to individuals, it could provide a biased estimate of the population-level use of a specific resource (Felicetti et al. 2003). The combination of both stable isotope and fecal analyses has been used successfully to estimate the diet of pygmy raccoons (*Procyon pygmaeus*—McFadden et al. 2006), long-nosed bandicoots (*Perameles nasuta*—Thums et al. 2005), mycophagous marsupials (McIlwee and Johnson 1998), and frugivorous bats (Herrera et al. 2001).

For stable isotope analysis we dried samples of potential foods at 60°C for 48 h and then ground the samples into a fine powder using a mixer mill (Retsch MM 200; Glen Mills Inc., Clinton, New Jersey). A subsample was placed into a miniature tin weighing boat (4 × 6 mm) for combustion and sent in duplicate to the University of Wyoming Stable Isotope Facility. Data of $\delta^{13}C$ and $\delta^{15}N$ were generated with a Costech ECS elemental analyzer (Costech Analytical Technologies, Valencia, California) attached to a Finnigan DeltaplusXP mass spectrometer (Thermo Fisher Scientific, Inc., Waltham, Massachusetts) using PeeDee Belemnite (PDB) for the C standard and atmospheric air for N. Sample results were accepted if variance between the 2 subsamples did not exceed 0.15‰ and machine linearity did not deviate from 0.99 (Ben-David et al. 1997). Blood samples collected from flying squirrels were processed similarly. For those samples serum was not separated from blood cells because of the small amount of blood collected in capillary tubes. Consequently, isotopic values for squirrels represent their diet over the 6–8 weeks prior to sampling.

We used multivariate analysis of variance (MANOVA—Zar 1999) and post hoc Scheffé multiple comparisons to test for significant differences in stable isotope values among the various diet items and assessed differences in isotope signatures using a *K*-nearest neighbor randomization test (Rosing et al. 1998). We tested for differences in isotopic values of whole blood between sexes using a Student's *t*-test assuming equal variance (Zar 1999). The isotope data for all distinct diet items and those of flying squirrels were incorporated into a dual-isotope linear mixing model to determine the relative contribution of the various diet items

to the overall squirrel diets in spring and autumn. For this analysis, we used the program SISUS (SISUS: Stable Isotope Sourcing Using Sampling—Erhardt 2007; Phillips and Gregg 2003) and analyzed data separately for spring and autumn. We corrected for diet–consumer discrimination by using a change of 1‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$ (DeNiro and Epstein 1981; Kelly 2000; McCutchan et al. 2003; Peterson and Fry 1987). We ran the model as concentration-dependent by including data on the composition of tissues of the different diet items because of large differences in C:N ratios (Phillips and Koch 2002) in lichens (37.9:0.7), truffles, (47.2:4.3), conifer seeds (53.5:1.6), and soil macroinvertebrates (48.2:12.4—M. Ben-David, pers. obs.).

We thawed fecal samples and placed 2 small portions from each pellet on a microscope slide. One drop of potassium hydroxide (KOH) was added to 1 portion of the sample and mixed vigorously using a razor blade. The other portion of the sample was mixed similarly with a drop of Melzer's solution. KOH is a standard rehydrating medium for mounting fungal spores, and Melzer's can aid in identification of certain fungal genera by reacting with the spore walls and ornamentation to produce a color reaction (Castellano et al. 1989). We covered the 2 samples with an 18 × 18-mm coverslip and examined the slide using bright-field microscopy at 100×, 400×, and 1,000×. We identified food items in the entire field of view for each coverslip (Mitchell 2001). Fungal spores were identified to genus using a spore key (Castellano et al. 1989). We calculated frequency of occurrence of the fungal taxa as the percentage of occurrence in the total number of fecal samples each season (Mitchell 2001; Pyare et al. 2002). We compared the number of genera per fecal sample to season and sex of squirrels using analysis of variance (ANOVA—Zar 1999).

Surveys of food availability and sampling of potential foods.—We used 20-m line transects, pitfall traps, and 1 × 1-m plots to estimate food availability in the 3 habitat types. We used preliminary data from initial surveys during the 1st field season to determine the number of transects required to detect differences in food availability among habitats with a statistical power of 0.90. Using Cohen's (1988:274) effect size index *F*-test for analysis of variance and covariance (Smith and Harke 2001) and a type I error rate equal to the type II error rate (0.10—Smith and Harke 2001), we established that 15 transects in each habitat would provide sufficient power to detect differences among habitats. We chose to measure 3 transects in each sampled stand to account for within-stand heterogeneity and ensure that each stand was properly represented in our sample. Accordingly, we conducted 135 line-transect surveys (3 surveys per stand × 15 stands per habitat × 3 habitat types). We conducted 90 line-transect surveys during the spring and 45 during the autumn. The inequality in surveys between seasons was due to logistical constraint and was not related to the power analysis.

Transect locations within each habitat and the azimuths of transects were chosen randomly. At each site we established transect lines with a compass. A field tape was used to estimate presence and abundance and frequency of occurrence of *Vaccinium* spp., arboreal lichens, and epigeous fungi by walking along the line and estimating the length of interception for each of the diet items considered. Following the survey and along each transect, 5 pitfall traps were installed to sample nonvolant soil macroinvertebrates. Pitfall traps were 473-ml plastic cups buried in the earth with the lip flush with the surface of the forest floor. A plastic plate was placed over each cup to exclude rainwater and to mimic debris that invertebrates seek for shelter. The traps remained in place for approximately 3 days at which point the contents were emptied into individual plastic bags and frozen until identification and further analysis in the laboratory at the University of Wyoming. A total of 225 traps was collected from each of the 3 habitat types for a total of 675 traps. In the laboratory, macroinvertebrates were identified at least to order using a dissection microscope and guide books (Borror and White 1970; Kaston et al. 1978; White 1983; White and Borror 1998).

At each of the line-transect survey sites we conducted 2 truffle surveys (spring) during 2004 and 4 (spring and autumn) during 2005. At each end of each transect (all seasons) and 10 m from the center of the line on each side (spring and autumn 2005) we established a 1 × 1-m plot for estimating availability of spruce and hemlock seeds and truffles. The placement of the grid was initially selected at random but subsequently modified to avoid trees, rocks, and densely vegetated areas. We attempted to place the grids under logs (10–70 cm in diameter) whenever possible to maximize encounters with truffles. We recorded and removed downed woody debris and counted spruce and hemlock cones on each plot. We used methods similar to those reported by Clarkson and Mills (1994) to estimate truffle biomass and chose sampling periods that coincided with spring and autumn truffle blooms (Colgan 1997). We used hand rakes and slowly raked the soil, from the surface of the duff to the organic–mineral soil interface. Unearthed truffles were identified to genus and weighed for fresh biomass. In all, we surveyed 150 truffle plots. While digging, we also counted all uncovered earthworms. We collected subsamples of the various potential food items (i.e., lichens, truffles, mushrooms, berries, conifer seeds, new conifer growth, and soil macroinvertebrates) and froze them for use later in stable isotope analysis.

To determine whether food availability of all items, except invertebrates, differed among habitat types and between seasons, we used a nested 2-way ANOVA (Zar 1999), where the main effects were stand (clear-cut, 2nd-growth, or old-growth) and transect (nested within stand) and Scheffé multiple comparison tests. To test for differences in the abundance of soil macroinvertebrates among habitats and seasons, we averaged the number of invertebrates in each trap (5 traps/line-transect survey) along each line transect and similarly used a 2-way ANOVA with stand, season (spring or autumn), and transect (nested within stand) as main effects. Because many of the invertebrates we collected were too small to serve as food for flying squirrels, we categorized the invertebrates as small (<2 mm in length excluding append-

Table 1.—Mean (± *SE*) $\delta^{13}C$ and $\delta^{15}N$ values (‰) and elemental concentrations of potential food items for northern flying squirrels (*Glaucomys sabrinus griseifrons*) on Prince of Wales Island, Alaska. Number of samples included in the global mean for calculating the $\delta^{13}C$ and $\delta^{15}N$ is given by *n*. Letters represent significant differences ($\alpha = 0.05$) in both $\delta^{13}C$ and $\delta^{15}N$ as determined from MANOVA followed by Scheffé post hoc multiple comparisons (Zar 1999) and K nearest-neighbors randomization tests (Rosing et al. 1998).

Diet item	*n*	$\delta^{13}C$	$\delta^{15}N$	Significance all items	Significance pooled items	Elemental concentration	
						% $\delta^{13}C$	% $\delta^{15}N$
Epigeous fungi	32	−24.49 ± 0.30	4.37 ± 0.55	ag	a	47.2	1.7
Truffles	35	−27.32 ± 0.18	4.48 ± 0.29	b	b	47.2	1.7
Hemlock seeds	20	−25.26 ± 0.25	−1.70 ± 0.67	c		53.5	1.6
Spruce seeds	14	−26.82 ± 0.30	−1.25 ± 0.57	d		53.5	1.6
Mean seeds	34	−25.90 ± 0.24	−1.51 ± 0.45		c	53.5	1.6
Lichens	23	−21.26 ± 0.28	−3.87 ± 0.25	e	d	37.9	0.7
Berries	8	−31.40 ± 0.45	0.29 ± 0.81	f	e	49.3	1.7
Araneidae	28	−25.45 ± 0.17	5.67 ± 0.24	g		48.2	12.4
Scaphinotus angusticollis	30	−26.73 ± 0.15	3.75 ± 0.33	bg		48.2	12.4
Pterostichus spp.	28	−26.49 ± 0.26	4.76 ± 0.25	g		48.2	12.4
Diplopoda	30	−24.36 ± 0.14	2.78 ± 0.32	a		48.2	12.4
Harpaphe hadeniana	30	−23.69 ± 0.15	3.08 ± 0.42	ag		48.2	12.4
Earthworms	17	−26.61 ± 0.15	4.24 ± 0.22	a		48.2	12.4
Mean invertebrates	133	−25.26 ± 0.12	3.84 ± 0.16		f	48.2	12.4

ages), medium (2–10 mm), and large (>10 mm). We then repeated the analysis (with a 2-way ANOVA) only for large macroinvertebrates.

Results

We captured and processed a total of 36, 45, 30, 39, and 50 individual flying squirrels during spring 2003, 2004, and 2005, and autumn 2004 and 2005, respectively. During autumn 2004 and 2005, we captured 15 and 23 juveniles, respectively. From those individuals, we collected a total of 39 blood samples with enough volume for stable isotope analysis: 15 during spring 2004, 9 during spring 2005, and 15 during autumn 2005. These samples were collected from 12 adult females and 27 adult males. We also collected 23, 17, 11, 20, and 11 fecal samples from unique individuals during spring 2003, 2004, and 2005, and autumn 2004 and 2005, respectively, for a total of 51 spring samples and 31 autumn samples. Fecal samples collected during the spring field seasons were all from adult squirrels. During autumn seasons of 2004 and 2005, respectively, we collected 2 and 4 fecal samples from juveniles. We collected both feces and blood samples from 20 individuals in quantities sufficient for both analyses.

Table 2.—Relative contribution (± *SD*) to the diet of northern flying squirrels (*Glaucomys sabrinus griseifrons*) during spring 2003–2005 and autumn 2004–2005 on Prince of Wales Island, Alaska, for diet items. Proportions of diet item in overall squirrel diet were estimated by a concentration-dependent, dual-isotope linear mixing model. To account for trophic discrimination, we added 1‰ $\delta^{13}C$ and 3‰ $\delta^{15}N$ to each source value before incorporating into the model (SISUS). We removed berries and invertebrates from the concentration-dependent linear mixing model because berry seeds were not observed in feces.

Diet item	Relative contribution	
	Spring	Autumn
Epigeous fungi	0.04 ± 0.03	0.10 ± 0.07
Truffles	0.04 ± 0.03	0.09 ± 0.06
Conifer seeds	0.43 ± 0.03	0.33 ± 0.05
Lichens	0.47 ± 0.02	0.43 ± 0.04
Invertebrates	0.02 ± 0.01	0.05 ± 0.04

Diet estimates from stable isotopic analyses.—We found significant differences in the $\delta^{13}C$ and $\delta^{15}N$ of all diet items ($P < 0.05$; Table 1), except among several invertebrates and epigeous fungi ($P > 0.05$; Table 1). Also, we found significant effects of habitat on the isotopic values of the different macroinvertebrates (E. A. Flaherty and M. Ben-David, pers. obs.). To ensure that we did not introduce bias to our diet estimates because flying squirrels on POW rarely venture into clear-cuts and 2nd-growth stands (S. Pyare and W. P. Smith, pers. obs.), in subsequent analyses we used the isotopic signatures of items collected in old-growth habitats only. After pooling large-sized soil macroinvertebrates into a single group, invertebrates and epigeous fungi differed isotopically (Table 1). The isotopic signature of that soil macroinvertebrate group was not significantly different ($P > 0.05$) from that of earthworms (Table 1). Although spruce and hemlock seeds also differed ($P < 0.05$) isotopically (Table 1), we used average $\delta^{13}C$ and $\delta^{15}N$ values of these 2 items to create a category called conifer seeds to reduce the number of food items relative to sample size of squirrels. Finally, we did not include berries in the model because this food item was never identified in our fecal analysis. Therefore, we introduced the following diet categories into a dual-isotope, concentration-dependent linear mixing model: epigeous fungi, truffles, conifer seeds, lichens, and soil macroinvertebrates (Tables 1 and 2; Fig. 2).

Isotopic values in whole blood of flying squirrels captured during spring were more variable than those captured during autumn (Fig. 2), suggesting greater variation in diet among individuals. These differences were not related to the sex of

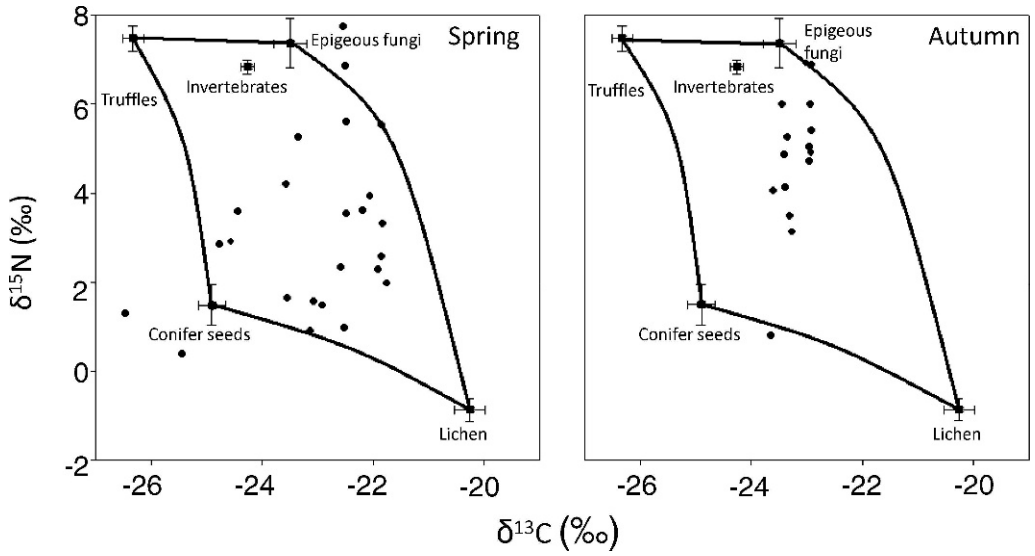

FIG. 2.—Distribution of isotopic values (mean ± *SE*) of potential foods and individual flying squirrels (*Glaucomys sabrinus griseifrons*) in spring and autumn on northern Prince of Wales Island, Alaska, for a concentration-dependent mixing model. The lines connecting potential food sources enclose the mixing space for the dual-isotope linear mixing models used to convert isotopic data to estimates of relative contribution. Although $\delta^{13}C$ and $\delta^{15}N$ values of several individual squirrels fell out of the mixing space, mean values were well within it in both autumn ($\delta^{13}C = -23.20‰ \pm 0.069‰$; $\delta^{15}N = 4.77‰ \pm 0.46‰$) and spring ($\delta^{13}C = -23.07‰ \pm 0.26‰$; $\delta^{15}N = 3.13‰ \pm 0.39‰$). We removed values for berries from the linear mixing model because berry seeds were not observed in feces.

the animals ($\delta^{13}C$: $t_{38} = 2.06$, $P = 0.63$; $\delta^{15}N$: $t_{38} = 2.06$, $P = 0.54$). During spring the $\delta^{13}C$ and $\delta^{15}N$ values of 4 of 24 individual squirrels fell out of the mixing space (Fig. 2), but only 1 of 15 did so in autumn. Such deviations likely resulted from our use of deterministic discrimination values rather than from pooling diet items (Table 1; Fig. 2). Using the population means, we estimated with the concentration-dependent mixing model that lichens had the largest contribution to the spring diets of northern flying squirrels (47%) followed by conifer seeds (43%), truffles (4%), and epigeous fungi (4%). During autumn, lichens again had the largest overall contribution to the diet (43%), followed by seeds (33%) and epigeous fungi (10%).

Fecal analysis.—We identified 10 different truffle genera and 2 taxa of epigeous fungi, Boletales and *Cortinarius* spp., with the latter more frequently consumed in autumn (Table 3). For truffles, *Elaphomyces* spp. were present in most samples (35–91%) and consumed in both seasons, followed by *Octaviania* (9–85%) and *Gymnomyces* (8–75%), which were largely consumed in autumn (Table 3). Of the other truffle genera, *Hydnotrya* was more prevalent in spring feces, whereas *Rhizopogon* and *Sarcosphaera* were consumed more frequently in autumn (Table 3). No significant difference ($F_{2,83} = 0.115$, $P = 0.736$) existed in the mean number of fungi genera consumed between males and females. Overall, truffles and lichens occurred most often in flying squirrel feces in both spring and autumn; truffle spores were found in 82–96% of the samples, whereas lichen material was found in 100% of the fecal samples during spring and ≥90% during autumn (Table 4). The next most common food item was

TABLE 3.—Percent occurrence of fungal spores in feces of northern flying squirrels (*Glaucomys sabrinus griseifrons*) on northern Prince of Wales Island, Alaska. Feces were collected from trapped individuals during spring 2003–2005 and autumn 2004–2005.

	% occurrence						
Fungus	Spring 2003	Spring 2004	Spring 2005	Spring $\bar{X}$ (*SE*)	Autumn 2004	Autumn 2005	Autumn $\bar{X}$ (*SE*)
Boletales[a]	0	0	0	0.0 (0.0)	50	29	39.5 (10.5)
Cortinarius[a]	0	0	8	2.7 (2.7)	75	24	49.5 (25.5)
Elaphomyces	91	77	83	83.7 (4.1)	35	53	44.0 (9.0)
Gautieria	13	0	0	4.3 (4.3)	0	0	0.0 (0.0)
Gymnomyces	26	0	8	11.3 (7.7)	75	53	64.0 (11.0)
Hydnotria	74	24	8	35.3 (19.9)	0	0	0.0 (0.0)
Hymenogaster	0	0	0	0.0 (0.0)	35	29	32.0 (3.0)
Hysterangium	0	12	0	4.0 (4.0)	5	0	2.5 (2.5)
Octavianina	30	6	17	17.7 (6.9)	85	59	72.0 (13.0)
Rhizopogon	0	6	0	2.0 (2.0)	15	29	22.0 (7.0)
Sarcosphaera	0	0	0	0.0 (0.0)	15	6	10.5 (4.5)
Tubers	9	0	0	3.0 (3.0)	0	0	0.0 (0.0)

[a] Epigeous fungi.

Table 4.—Percent occurrence of food items in feces of northern flying squirrels (*Glaucomys sabrinus griseifrons*) from old-growth Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) stands on northern Prince of Wales Island (POW), Alaska. These data are compared with diet estimates from fecal analysis of flying squirrels from other portions of Prince of Wales Island from Pyare et al. (2002). n = sample size of unique squirrels.

			% occurrence					No. truffle genera
	Season	n	Truffles	Lichens	Vegetation	Epigeous fungi	Invertebrates	
Northern POW	Spring 2003	23	96	100	91	0	0	7
	Spring 2004	17	82	100	77	0	12	5
	Spring 2005	12	83	100	92	8	0	5
	Spring $\bar{X}$ (*SE*)		87.0 (4.5)	100.0 (0.0)	86.7 (4.8)	2.7 (2.7)	4.0 (4.0)	5.7 (0.7)
	Autumn 2004	20	95	90	70	70	0	8
	Autumn 2005	17	82	94	82	53	12	7
	Autumn $\bar{X}$ (*SE*)		88.5 (6.5)	92.0 (2.0)	76.0 (6.0)	61.5 (8.5)	6.0 (6.0)	7.5 (0.5)
Pyare et al. 2002	Summer–autumn	150	50.4	27.0	55.2	36.1	4.4	3.0

vegetation, which was equally consumed in both seasons, followed by epigeous fungi, which were largely consumed in autumn (Table 4). Soil macroinvertebrates, specifically wing parts, also were present, although infrequently, in feces from both seasons (Table 4).

Food availability.—In general, availability of potential food items for flying squirrels did not differ ($P > 0.05$) seasonally, except for hemlock and spruce seeds and *Vaccinium* spp. (Table 5), which were approximately 2.5 ($\bar{X} \pm SE$, 261 ± 22 cones in spring versus 104 ± 29 cones in autumn) and 2.9 (13 ± 4 cones in spring versus 5 ± 2 cones in autumn) times more available during spring in old-growth for hemlock and spruce cones, respectively, whereas *Vaccinium* was more available in autumn (526.97 ± 75.35 cm in spring versus 714.13 ± 95.20 cm in autumn; Table 5). Transects in old-growth forest stands had 30 times more spruce cones than managed habitats (Table 5). Hemlock cones were 20 times more abundant in old-growth compared with 2nd-growth stands and 9 times more abundant than in clear-cuts (Table 5). Similarly, *Vaccinium* spp. were 2–3 times more common in old-growth (Table 5) than in managed habitats (Table 5). We found no truffles in 2nd-growth stands; truffles were about 2.5 times more abundant in old-growth plots than in clear-cuts ($P = 0.034$). Similarly, there was twice as much lichen in old-growth stands than in clear-cuts and 9 times more than in 2nd-growth stands (Table 5; $P = 0.002$). We found no difference ($P > 0.05$) in the abundance of epigeous fungi among habitats (Table 5). In all surveys of truffles we identified only the genus *Elaphomyces*, which in some of the 1-m^2 plots in old-growth forest reached a total biomass of 32 g.

We collected >3,700 soil macroinvertebrate specimens, which were identified to 13 taxa: Acari, Araneida, Coleoptera, Collembola, Diplopoda, Diptera, Gastropoda, Hymenoptera, Isopoda, Isoptera, Oligochaeta, Opiliones, and Scolopendromorpha. Acarina and Coleoptera were the most abundant orders, comprising >33% and >23% of macroinvertebrates sampled, respectively. Traps along transects in 2nd-growth stands had significantly more soil macroinvertebrates than the other 2 habitats; clear-cuts had the fewest invertebrates ($F_{2,675} = 10.225$, $P = 0.006$; Fig. 3).

After excluding the small (Araneidae, Collembola, Acari, Diptera, and Opiliones) and medium-sized (Buprestidae [Coleoptera], Curculionidae, Isoptera, Gastropoda, and Hymenoptera) invertebrates, analyses revealed that of the large invertebrates (Araneidae [spiders], Chilopoda [centipede], *Scaphinotus angusticollis* and *Pterostichus* spp. [Coleoptera],

Table 5.—Abundance, measured as biomass (g), count (no.), or length of transect intersected (cm) of potential food items from spring (2004–2005) and autumn (2005) surveys on Prince of Wales Island, Southeast Alaska. In each of 15 stands per habitat we conducted 3 surveys for a total of 135 line-transects. We report *P*-values (statistically significant in bold) from a nested ANOVA for comparing availability of food between stands and differences in availability between spring and autumn.

	Habitat ($\bar{X} \pm SE$)						Comparison	
	Clear-cut		Second-growth		Old-growth			
Food item	Spring	Autumn	Spring	Autumn	Spring	Autumn	Between-stands *P*-value	Between-seasons *P*-value
Epigeous fungi (cm)	0.83 ± 0.46	0.33 ± 0.23	0.20 ± 0.20	1.13 ± 0.81	0.23 ± 0.18	2.53 ± 1.43	0.46	0.42
Truffles (g)	0.77 ± 0.57	0.55 ± 0.36	0	0	1.95 ± 0.61	1.03 ± 0.77	**0.00**	0.28
Hemlock cones (no.)	21.55 ± 13.70	11.57 ± 4.32	3.21 ± 1.73	20.55 ± 11.87	261.25 ± 22.07	103.98 ± 28.94	**0.01**	**0.00**
Spruce cones (no.)	0.35 ± 0.13	0.12 ± 0.06	0.27 ± 0.12	0.32 ± 0.12	12.93 ± 3.84	4.47 ± 2.15	**0.03**	**0.046**
Lichens (cm)	1.10 ± 0.68	2.47 ± 1.55	0.50 ± 0.50	0	3.83 ± 1.53	1.13 ± 0.84	**0.03**	0.38
Vaccinium (cm)	198.50 ± 42.60	249.87 ± 59.57	511.50 ± 18.63	72.2 ± 18.63	526.97 ± 75.97	714.13 ± 95.20	**0.00**	**0.04**
New spruce growth (cm)	15.80 ± 8.92	0	7.67 ± 5.46	0	13.33 ± 13.33	0	0.85	0.07

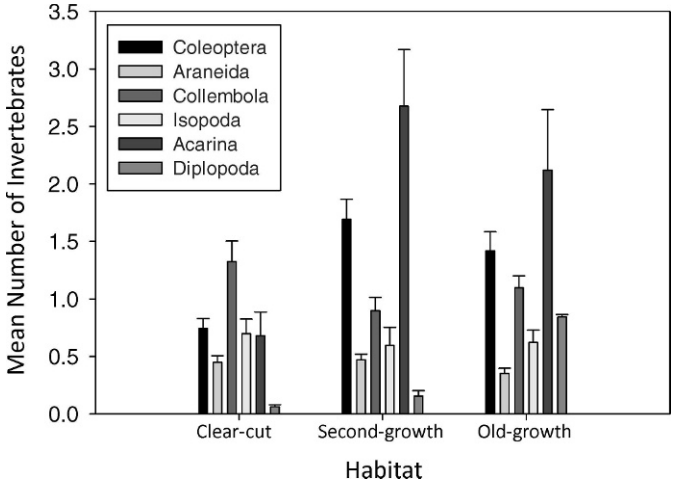

FIG. 3.—Mean (± *SE*) number of soil macroinvertebrates captured in pitfall traps along 135 transects on Prince of Wales Island, Alaska, in the 3 habitat types: clear-cut, 2nd-growth, and old-growth. The 6 major groups of invertebrates (>5 individual invertebrates were sampled) are shown.

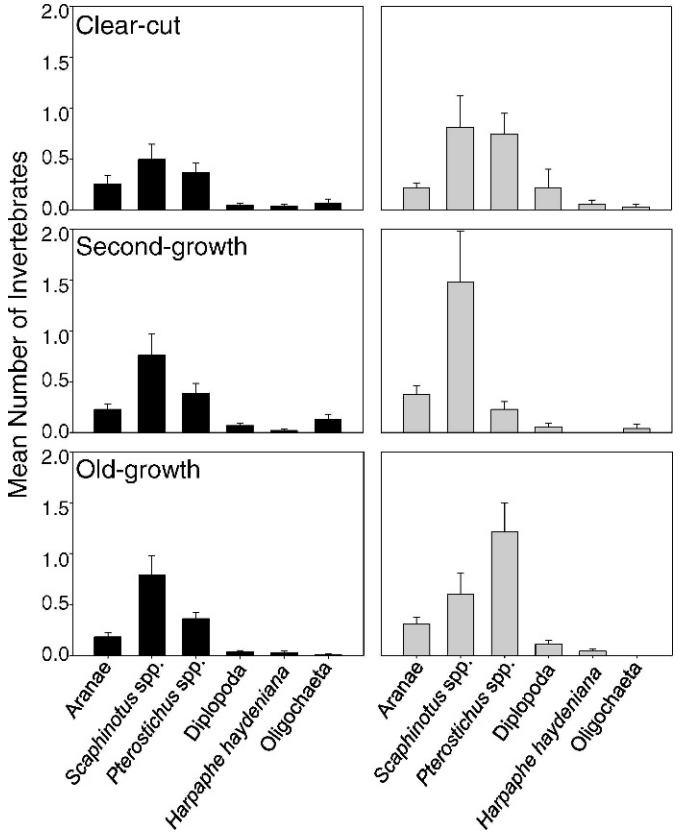

FIG. 4.—Mean (± *SE*) number of 6 large (>10 mm in body length) soil macroinvertebrates sampled in pitfall traps on Prince of Wales Island, Alaska, in the 3 habitat types clear-cut, 2nd-growth, and old-growth, in the spring (black bars) and the autumn (gray bars). These represent the most likely invertebrates consumed by northern flying squirrels (*Glaucomys sabrinus griseifrons*).

Diplopoda [e.g., a small, black millipede and *Harpaphe hadeniana*], and Oligochaeta [earthworms]), only *S. angusticollis* and *Pterostichus* spp. were more abundant in 2nd-growth stands than in other habitats ($F_{2,673} = 9.539$, $P = 0.008$, and $F_{2,673} = 9.446$, $P = 0.008$, respectively; Fig. 4). Oligochaetes were more available in clear-cuts ($F_{2,673} = 9.266$, $P = 0.008$; Fig. 4). No consistent seasonal differences in the number of large soil macroinvertebrates were found among the 3 habitat types (Fig. 4).

DISCUSSION

Both stable isotope and fecal analyses revealed that arboreal lichens, conifer seeds, and fungal sporocarps were the main dietary items consumed and assimilated by *G. sabrinus* on POW. Both analyses also highlighted the increased importance of fungi, especially epigeous fungi, during autumn, and lichens during spring. Similarly, both methods revealed that vegetation, likely in the form of conifer seeds, and soil macroinvertebrates were consumed by squirrels, whereas berries were not. Finally, using both methods we did not detect any differences in diet between the sexes. The main disagreement between the 2 methods was the contribution and importance of truffles. Although examination of stable isotope data suggested that squirrels assimilated few nutrients from truffles (especially N), truffle spores were among the most frequent diet items in feces. It is possible that squirrels frequently consumed truffles but little N was assimilated from this food source.

The discrepancy between results from stable isotopes and fecal analyses potentially could be explained by our use of data only for *Elaphomyces* spp. to represent the isotopic values of all truffles. It is possible that other truffles consumed by *G. s. griseifrons* have different isotopic signatures and that their inclusion would have changed our results. Several animals during both spring and autumn had values that were not included in the isotopic mixing space. Although such misalignment of consumer and diet items could result from effects of habitat use (E. A. Flaherty and M. Ben-David, pers. obs.), diet quality, elemental routing, tissue-turnover rates, and variation in the length of the assimilation period (Karasov and Martinez del Rio 2007), this misalignment most commonly occurs when potential foods are excluded (Newsome et al. 2007). Nonetheless, because relatively few animals were misaligned with the mixing space, and overall the isotopic signatures of both mushrooms and truffles were similar (especially in ^{15}N), it is not likely that our results would have changed dramatically had we sampled other truffles. It is important to note here that we did not analyze other truffle species for stable isotopes because we encountered none during our surveys.

Alternatively, it is possible that although *G. sabrinus* consumes large quantities of truffles, when these squirrels are limited to *Elaphomyces* spp. they may assimilate little of this resource. Past research indicates that movements, population density (Gomez et al. 2005; Pyare and Longland 2002; Waters and Zabel 1995), survival, and recruitment (Lehmkuhl et al. 2006) of *G. sabrinus* are correlated directly

with availability of truffles. However, when consumed as the sole food source, *Elaphomyces* has minimal nutritional value for *G. sabrinus* (Cork and Kenagy 1989), other small mammals are unable to maintain body mass when consuming this resource (Cork and Kenagy 1989; Dubay et al. 2008), and in areas and seasons with high species richness, *G. sabrinus* will not consume *Elaphomyces* (Meyer et al. 2005). Thus, the dominance of *Elaphomyces* in our sampling plots and in the feces suggests that flying squirrels on POW likely assimilated few nutrients from the majority of truffles they consumed. Moreover, past work indicates that most of the N found in truffles is indigestible by flying squirrels and other small mammals (Claridge and Cork 1994; Claridge et al. 1999; Cork and Kenagy 1989); other nutrients, such as potassium, phosphorous, and vitamin D, that occur in *Elaphomyces* may explain the preference for this diet item (Dubay et al. 2008). Similarly, although low in N, fiber, lipids, and other important nutrients (Dubay et al. 2008), arboreal lichens are high in calcium (Ca) and have high digestibility (Robbins 1987). It is possible that flying squirrels consume high amounts of lichen to maintain Ca uptake and include other diet item such as conifer seeds, invertebrates, and epigeous fungi to mitigate the low availability of N and other nutrients in truffles and lichens; mixed diets are common among mycophagist mammals (McIlwee and Johnson 1998; Orrock and Pagels 2002).

Our dietary estimates from both fecal and isotope analyses contrast with some findings of previous research in Southeast Alaska (Pyare et al. 2002) and are more similar to diets reported for *G. sabrinus* in other parts of its range (Smith 2007), where typically 100% of fecal samples contained fungal spores (Rosentreter et al. 1997; Wheatley 2007). Pyare et al. (2002) identified truffle spores in 50.4% of their autumn samples compared to $\geq$82% in this study. Furthermore, our analysis indicated that flying squirrel diets in the northern part of POW contained a greater diversity of truffle genera than reported by Pyare et al. (2002). They identified only 3 genera (mostly *Elaphomyces*, and some *Hymenogaster* and *Sclerogaster*), whereas we identified a minimum of 5–8 genera. Similarly, whereas both stable isotopes and fecal analyses identified lichens as an important food source, Pyare et al. (2002) reported that only 27% of their samples contained lichens. In addition, Pyare et al. (2002) encountered relatively few epigeous fungal spores in their sample of squirrel feces, whereas we estimated this to be an important resource for flying squirrels in autumn. It is possible that the differences in dietary estimates between the 2 studies on POW stem from timing of sampling; Pyare et al. (2002) collected their samples mainly during summer, whereas we sampled squirrels during spring and autumn. Future studies that include all seasons may better elucidate the factors responsible for the divergent dietary estimates of these 2 studies.

The higher variation in diet among individual squirrels during spring corresponded with higher consumption of conifer seeds. In conifers a new crop of cones is produced in summer (Koenig and Knops 2000), and although flying squirrels rarely harvest and cache cones in middens like red squirrels (*Tamiasciurus hudsonicus*—Mowery and Zasada 1984), they likely are able to reach these newly developing cones in autumn. Therefore, it is surprising that conifer seeds were more prominent in spring than autumn diets. We suspect that the higher consumption of conifer seeds during spring is a function of lower availability of truffles, other than *Elaphomyces*, during this time of year. Although we did not encounter any such truffles in our plots in either spring or autumn, the higher occurrence of *Gymnomyces*, *Hymenogaster*, *Octavianina*, *Rhizopogon*, and *Sarcosphaera* in feces during autumn suggests that they were more abundant at that time of year. Given this observation and equal abundance of mushrooms during spring and autumn, it is surprising that squirrels consumed more mushrooms during autumn. Whether autumn mushrooms provide better nutritional value for flying squirrels than those developing in spring is unknown and merits further investigation.

Our dietary data are based on samples collected from animals captured in old-growth stands only. It is possible that we would have drawn different conclusions had we sampled flying squirrels in 2nd-growth stands. Past work has indicated that 2nd-growth habitats can support populations of flying squirrels in other parts of their range (Ransome et al. 2004; Ransome and Sullivan 2003; Wheatley et al. 2005). Nonetheless, Smith (2007) cautioned that population density may not be a reliable indicator of habitat quality. Results from a study on POW comparing flying squirrel use of peatland–mixed conifer to old-growth habitats initially indicated that the number of reproductive females was greater in peatland–mixed conifer stands than in old-growth stands and that recruitment was only slightly lower in the former (Smith and Nichols 2003). However, later population modeling indicated that peatland-mixed conifer stands actually functioned as population sinks (Smith and Person 2007). Moreover, perceptual range and fine-scale movement data (Flaherty et al. 2008), energetics measurements related to the costs of running versus gliding (E. A. Flaherty, pers. obs.), telemetry data, and dispersal modeling (S. Pyare and W. P. Smith, pers. obs.) indicate that northern flying squirrels on POW actively avoid 2nd-growth stands.

Our results suggest low availability of potentially critical food items in managed habitats, which may constrain dispersal of *G. sabrinus* across clear-cut and 2nd-growth habitats. Conifer seeds, truffles, and *Vaccinium* spp. were all significantly more abundant in old-growth habitat. Furthermore, the hemlock and spruce cones we sampled in clear-cuts were likely remnants of the once present old-growth stand and consequently are likely only available for a short time postlogging. Similarly, although we encountered truffles in clear-cut plots, it is unclear how available this resource is in young regenerating stands, because we found truffles only where the roots of tree stumps had not completely died; we recorded no truffles in clear-cuts older than 2–3 years postharvest. Except for 1 sporocarp uncovered while digging a pitfall trap in a $>$40-year-old stand, we found no truffles in

2nd-growth habitat. Carey et al. (2002) suggested that harvest plans that leave legacy (i.e., old-growth trees) in managed stands will increase the persistence of truffles. This has not been the prescribed management practice in more than 4 decades of logging POW (United States Department of Agriculture Forest Service 1997), nor is it clear if legacy retention will achieve this objective because of the vulnerability of leave trees to windthrow (Concannon 1995). We do acknowledge that our truffle survey technique likely was inadequate to detect the majority of genera because we were only able to uncover 1 of 8 consumed by the squirrels. Nonetheless, the low occurrence of 5 of these genera in the feces of squirrels (especially in spring) suggests that they were rare even in old-growth habitats. Future work should consider using a trained, truffle-detecting dog for line-transect surveys or increasing survey intensity.

Availability of mushrooms and lichens, both important diet items during autumn, was similar in old-growth and clear-cut stands. Nonetheless, both were lower in 2nd-growth habitats that comprise the majority of the managed landscape on POW because of declining frequency of timber harvest in recent years. That lichens were less available in 2nd-growth stands suggests that the lichens found in clear-cuts likely remained from felled trees during the harvest rather than having been blown in from adjacent old-growth stands. Lichens surveyed in clear-cuts were desiccated and appeared older than those surveyed in old growth. Consequently, this resource (like conifer cones) will be available only during a brief period after logging.

Conversely, soil macroinvertebrates, especially those larger than 10 mm, were more abundant in managed habitats than in old-growth stands. Soil moisture is presumably lower in clear-cuts and some 2nd-growth habitats because of the absence of a developed canopy, which affects decomposition, evaporation, and other soil characteristics that influence habitat use by soil invertebrates (Niemelä 1997). Given our relatively high estimates of proportion of soil macroinvertebrates from stable isotope analyses during both spring and autumn, it appears as though flying squirrels dispersing through the managed matrix potentially could replenish depleted energy stores by consuming invertebrates. However, examination of feces indicated that none of the most abundant invertebrates actually were consumed by flying squirrels. Rather, invertebrate remains in feces were small wing parts likely from flies that were consumed coincidentally when flying squirrels fed on mushrooms. Thus, the high abundance of soil macroinvertebrates in managed habitats likely would not improve the foraging success of dispersing flying squirrels.

The high proportion of 2nd-growth stands in the managed matrix on POW, the lack of truffles in those stands and their limited temporal availability in clear-cuts, and the relatively low availability of other alternative foods likely will result in low encounter rates by dispersing squirrels. Low encounter rates with food resources will cause squirrels to commit additional time to foraging in this high-cost environment. The extent to which increased foraging time directly influences dispersal success is unclear, but increasing search time will presumably increase predation risk because flying squirrels could not launch into evasive glides in clear-cut and 2nd-growth stands that lack tall trees while increasing energy expenditure in unfamiliar and structurally deficient habitats (E. A. Flaherty, pers. obs.). Further work is needed to explore the relationship between predation risk and stand age in managed forests.

In conclusion, despite the varied diet of *G. sabrinus* in Southeast Alaska, availability of potential foods is low in managed habitats compared to old-growth forest. Therefore, continued loss of such stands from timber harvest might cause further decline in overall food availability across managed landscapes. Food resources, which were significantly lower in managed stands on POW, are among the most significant factors limiting populations of *G. sabrinus* (Lehmkuhl et al. 2006; Ransome and Sullivan 1997; Smith 2007) and affect reproduction, survival, recruitment, space use, habitat core-use areas, and home-range size (Holloway 2006; Menzel et al. 2004). Because natal and adult breeding dispersal in managed rain forests on POW require that flying squirrels move long distances (Smith et al., in press), these animals likely will encounter clear-cut and 2nd-growth stands. Although these high-cost habitats might not completely eliminate flying squirrel dispersal, the substantially lower permeability of managed stands (Smith et al., in press) could significantly reduce survival and dispersal success (Ransome and Sullivan 2003).

Low use of early seral habitats by flying squirrels could reduce the dissemination of fungal spores into managed stands (Pyare and Longland 2001). Although low soil moisture (Harvey et al. 1979; Luoma et al. 1991) and decreased abundance of coarse woody debris are responsible for the low production of truffles in the managed stands (Amaranthus et al. 1994; Clarkson and Mills 1994), lower inoculation rates of tree roots (Pyare and Longland 2001) could add to the slower rates of fungal establishment in early seral forests. Because the small mammal fauna of Southeast Alaska is depauperate (MacDonald and Cook 1996), few alternative mycophagists are available to serve as spore vectors. Thus, the persistence of flying squirrels in managed landscapes may be necessary to ensure the timely inoculation and reestablishment of colonies of ectomycorrhizal fungi that promote forest development (Carey et al. 1999). Arguably, ensuring the proliferation of mycorrhizal fungi in managed landscapes is important for regenerating timber resources. Nevertheless, without adequate food resources, the ability of flying squirrels to replenish energy stores while dispersing across 2nd-growth and clear-cut habitats may be limited, and populations in managed landscapes are at risk of becoming isolated. Without dispersal, the persistence of *G. sabrinus* in managed landscapes is uncertain (Smith and Person 2007).

Acknowledgments

We thank I. Abernathy, C. Boser, L. Bruner, D. Caton, R. Choi, D. Haynes, K. Keffer, K. Leonard, K. Lunde, S. Scott, C. Shanley, K.

Van Dyke, and G. Yenni and all of our Earthwatch volunteers for field assistance. S. L. Miller assisted with the identification of fungal spores. M. Clementz, M. Castellano, and 2 anonymous reviewers provided helpful comments on earlier versions of the manuscript. Funding and logistical support were provided by the United States Fish and Wildlife Service, United States Forest Service, Earthwatch, Denver Zoological Foundation, and the University of Wyoming.

Literature Cited

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce–western hemlock forests of Southeast Alaska. Ecology 63:1932–1948.

Amaranthus, M., J. M. Trape, L. Bednat, and D. Arthur. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. Canadian Journal of Forest Research 24:2157–2165.

Angerbjörn, A., P. Hersteinsson, K. Lidén, and E. Nelson. 1994. Dietary variation in arctic foxes (*Alopex lagopus*)—an analysis of stable carbon isotopes. Oecologia 99:226–232.

Ben-David, M., R. W. Flynn, and D. M. Schell. 1997. Annual and season changes in diets of martens: evidence from stable isotope analysis. Oecologia 111:280–291.

Ben-David, M., and D. M. Schell. 2001. Mixing models in analyses of diet using multiple stable isotopes: a response. Oecologia 127:180–184.

Borror, D. J., and R. E. White. 1970. A field guide to the insects of America north of Mexico. Houghton Mifflin, Boston, Massachusetts.

Carey, A. B., W. Colgan III, J. M. Trappe, and R. Molina. 2002. Effects of forest management on truffle abundance and squirrel diets. Northwest Science 76:148–157.

Carey, A. B., J. Kershner, B. Biswell, and L. Domínguez de Toledo. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged stands. Wildlife Monographs 142:3–71.

Castellano, M., J. M. Trappe, Z. Maser, and C. Maser. 1989. Key to the spores of hypogeous fungi of northern temperate forests with special reference to animal mycophagy. Mad River Press, Eureka, California.

Claridge, A.W., and S. J. Cork. 1994. Nutritional value of two species of hypogeal fungi for the long-nosed potoroo (*Potorous tridactylus*), a forest dwelling mycophagous marsupial. Australian Journal of Zoology 42:701–710.

Claridge, A. W., J. M. Trappe, S. J. Cork, and D. L. Claridge. 1999. Mycophagy by small mammals in the coniferous forests of North America: nutritional value of sporocarps of *Rhizopogon vinicolor*, a common hypogeous fungi. Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology 169:172–178.

Clarkson, D. A., and L. S. Mills. 1994. Hypogeous sporocarps in forest remnants and clearcuts in southwest Oregon. Northwest Science 68:259–265.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences. 2nd ed. Lawrence Erlbaum Associates, Hillsdale, New Jersey.

Colgan, W. 1997. Diversity, productivity, and mycophagy of hypogeous mycorrhizal fungi in a variably thinned Douglas-fir forest. Ph.D. dissertation, Oregon State University, Corvallis.

Concannon, J. A. 1995. Characterizing structure, microclimate, and decomposition of peatland, beachfront, and newly-logged forest edges in southeastern Alaska. Ph.D. dissertation, University of Washington, Seattle.

Cork, S. J., and G. J. Kenagy. 1989. Nutritional value of hypogeous fungus for a forest-dwelling ground squirrel. Ecology 70:577–586.

Currah, R. S., E. A. Smreciu, T. Lehesvirta, M. Niemi, and K. W. Larsen. 2000. Fungi in the winter diets of northern flying squirrels and red squirrels in the boreal mixedwood forest of northeastern Alberta. Canadian Journal of Botany 78:1514–1520.

DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica Cosmochimica Acta 45:341–351.

Dubay, S. A., G. D. Hayward, and C. Martinez del Rio. 2008. Nutritional value and diet preference of arboreal lichens and hypogeous fungi for small mammals in the Rocky Mountains. Canadian Journal of Zoology 86:851–862.

Erhardt, E. B. 2007. SISUS: Stable Isotope Sourcing using Sampling. http://statacumen.com/sisus. Accessed 15 November 2007.

Felicetti, L. A., et al. 2003. Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears. Canadian Journal of Zoology 81:763–770.

Flaherty, E. A., W. P. Smith, M. Ben-David, and S. Pyare. 2008. Experimental trials of the northern flying squirrel (*Glaucomys sabrinus*) traversing managed rainforest landscapes: perceptual range and fine-scale movements. Canadian Journal of Zoology 86:1050–1058.

Gannes, L. Z., C. Martinez del Rio, and P. Koch. 1998. Natural abundance variations in stable isotopes and their potential uses in animal physiology ecology. Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 119:725–737.

Gannes, L. Z., D. O'Brien, and C. Martinez del Rio. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. Ecology 78:1271–1276.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for use of wild mammals in research. Journal of Mammalogy 88:809–823.

Gomez, D. M., R. G. Anthony, and J. P. Hayes. 2005. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. Journal of Wildlife Management 69:1670–1682.

Harvey, A. E., M. J. Larsen, and M. F. Juergensen. 1979. Comparative distribution of ectomycorrhizae in soils of three western Montana forest habitat types. Forest Science 25:350–358.

Herrera, L. G., K. A. Hobson, A. Manzo, D. Estrada, V. Sanchez-Cordero, and G. Mendez. 2001. The role of fruits and insects in the nutrition of frugivorous bats: evaluating the use of stable isotope methods. Biotropica 33:520–528.

Hilderbrand, G. V., S. D. Farley, C. T. Robbins, T. A. Hanley, K. Titus, and C. Servheen. 1996. Use of stable isotopes to determine diets of living and extinct bears. Canadian Journal of Zoology 74:2080–2088.

Hobson, K. A., and R. G. Clark. 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. Auk 110:638–641.

Holloway, G. 2006. Flying squirrel (*Glaucomys sabrinus* and *G. volans*) habitat use and ecology in landscapes managed with partial harvesting silviculture in central Ontario. Ph.D. dissertation, University of Toronto, Toronto, Ontario, Canada.

Howell, A. H. 1934. Description of a new race of flying squirrel from Alaska. Journal of Mammalogy 15:64.

KARASOV, W. H., AND C. MARTINEZ DEL RIO. 2007. Physiological ecology: how animals process energy, nutrients, and toxins. Princeton University Press, Princeton, New Jersey.

KASTON, B., J. BAMRICK, E. T. CAWLEY, AND W. G. JAQUES. 1978. How to know the spiders. McGraw-Hill, Boston, Massachusetts.

KELLY, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian ecology. Canadian Journal of Zoology 78:1–27.

KOENIG, W. D., AND J. M. H. KNOPS. 2000. Patterns of annual seed production by Northern Hemisphere trees: a global perspective. American Naturalist 155:59–69.

LEHMKUHL, J. F., L. E. GOULD, E. CÁZARES, AND D. R. HOSFORD. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. Forest Ecology and Management 200:51–65.

LEHMKUHL, J. F., K. D. KISTLER, J. S. BEGLEY, AND J. BOULANGER. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications 16:584–600.

LUOMA, D. L., R. E. FRENKEL, AND J. M. TRAPPE. 1991. Fruiting of hypogeous fungi in Oregon Douglas-fir forests: seasonal and habitat variation. Mycologia 83:335–353.

MACDONALD, S. O., AND J. A. COOK.1996. The land mammal fauna of Southeast Alaska. Canadian Field Naturalist 110:571–598.

MASER, C., Z. MASER, J. W. WITT, AND G. HUNT. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Canadian Journal of Zoology 64:2086–2089.

MASER, Z., C. MASER, AND J. M. TRAPPE. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Canadian Journal of Zoology 63:1084–1087.

MCCOLL, C. J., AND R. BOONSTRA. 1999. Physiological effects of three inhalant anesthetics on arctic ground squirrels. Wildlife Society Bulletin 27:946–951.

MCCUTCHAN, J. H., JR., W. M. LEWIS, JR., C. KENDALL, AND C. C. MCGRATH. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390.

MCFADDEN, W. K. W., R. N. SAMBROTTO, R. A. MEDELLÍN, AND M. E. GOMPPER. 2006. Feeding habits of endangered pygmy raccoons (*Procyon pygmaeus*) based on stable isotope and fecal analyses. Journal of Mammalogy 87:501–509.

MCILWEE, A. O., AND C. N. JOHNSON. 1998. The contribution of fungus to the diets of three mycophagous marsupials in *Eucalyptus* forests, revealed by stable isotope analysis. Functional Ecology 12:223–231.

MENZEL, J. M., W. M. FORD, J. W. EDWARDS, AND M. A. MENZEL. 2004. Nest tree use by the endangered Virginia northern flying squirrel in the central Appalachian Mountains. American Midland Naturalist 151:355–368.

MEYER, M. D., M. P. NORTH, AND D. A. KELT. 2005. Fungi in the diets of northern flying squirrels and lodgepole chipmunks in the Sierra Nevada. Canadian Journal of Zoology 83:1581–1589.

MITCHELL, D. 2001. Spring and fall diet of the endangered West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). American Midland Naturalist 146:439–443.

MOWERY, R. A., AND J. C. ZASADA. 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. Pp. 351–356 in Fish and wildlife relationship in old growth forests. Proceedings of a symposium held in Juneau, Alaska, April 12–15, 1982 (W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley, eds.). American Institute of Fishery Research Biologists, Morehead City, North Carolina.

NEWSOME, S. D., C. MARTINEZ DEL RIO, S. BEARHOP, AND D. L. PHILLIPS. 2007. A niche for isotopic ecology. Frontiers in Ecology 5:429–436.

NIEMELÄ, J. 1997. Invertebrates and boreal forest management. Conservation Biology 11:601–610.

ORROCK, J. L., AND J. F. PAGELS. 2002. Fungus consumption by the southern red-backed vole (*Clethrionomys gapperi*) in the southern Appalachians. American Midland Naturalist 147:413–418.

PETERSON, B. J., AND B. FRY. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320.

PHILLIPS, D. L., AND J. W. GREGG. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261–269.

PHILLIPS, D. L., AND P. L. KOCH. 2002. Incorporating concentration dependence in stable isotope mixing models. Oecologia 130:114–125.

PYARE, S., AND W. S. LONGLAND. 2001. Patterns of ectomycorrhizal fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. Journal of Mammalogy 82:681–689.

PYARE, S., AND W. S. LONGLAND. 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. Canadian Journal of Forest Research 32:1016–1024.

PYARE, S., W. P. SMITH, AND J. A. COOK. 2002. Diets of northern flying squirrels, *Glaucomys sabrinus*, in Southeast Alaska. Canadian Field-Naturalist 116:98–103.

RANSOME, D. B., P. M. F. LINDGREN, D. S. SULLIVAN, AND T. P. SULLIVAN. 2004. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest. I. Population dynamics of northern flying squirrels and red squirrels. Forest Ecology and Management 202:355–367.

RANSOME, D. B., AND T. P. SULLIVAN. 1997. Food limitation and habitat preference of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus*. Journal of Mammalogy 78:538–549.

RANSOME, D. B., AND T. P. SULLIVAN. 2003. Population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in old-growth and second-growth stands of coastal coniferous forests. Canadian Journal of Forest Research 33:587–596.

ROBBINS, C. T. 1987. Digestibility of an arboreal lichen by mule deer. Journal of Range Management 40:491–492.

ROSENTRETER, R., G. D. HAYWARD, AND M. WICKLOW-HOWARD. 1997. Northern flying squirrel seasonal food habits in the interior conifer forests of central Idaho, USA. Northwest Science 71:97–102.

ROSING, M. N., M. BEN-DAVID, AND R. P. BERRY. 1998. Analysis of stable isotope data: a K nearest-neighbors randomization test. Journal of Wildlife Management 62:380–388.

SMITH, W. P. 2007. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. Journal of Mammalogy 88:862–881.

SMITH, W. P., AND V. L. HARKE. 2001. Marbled murrelet surveys: site and annual variation, sampling effort, and statistical power. Wildlife Society Bulletin 29:568–577.

SMITH, W. P., AND J. V. NICHOLS. 2003. Demography of the Prince of Wales flying squirrel, an endemic of southeastern Alaska temperate rain forest. Journal of Mammalogy 84:1044–1058.

SMITH, W. P., AND D. K. PERSON. 2007. Estimated persistence of northern flying squirrel population in temperate rain forest fragments of Southeast Alaska. Biological Conservation 137:626–636.

SMITH, W. P., D. K. PERSON, AND S. PYARE. In press. Source–sinks, metapopulations, and forest reserves: conserving northern flying squirrels in the temperate rainforests of Southeast Alaska. In

Source, sinks, and sustainability across landscapes (J. Liu, V. Hull, A. T. Morzillo, and J. Weins, eds.). Cambridge University Press, Cambridge, United Kingdom.

THUMS, M., M. KLAASSEN, AND I. D. HUME. 2005. Seasonal changes in the diet of the long-nosed bandicoot (*Perameles nasuta*) assessed by analysis of faecal scats and of stable isotopes in blood. Australian Journal of Zoology 53:87–93.

THYSELL, D. R., L. J. VILLA, AND A. B. CAREY. 1997. Observations of northern flying squirrel feeding behavior: use of non-truffle food items. Northwestern Naturalist 78:87–92.

UNITED STATES DEPARTMENT OF AGRICULTURE FOREST SERVICE. 1997. Land and resource management plan—Tongass National Forest. United States Forest Service, Alaska Region, Juneau, R10-MB-338dd:1-1–L-1.

WATERS, J. R., K. S. MCKELVEY, C. J. ZABEL, AND W. W. OLIVER. 1994. The effects of thinning and broadcast burning on sporocarp production of hypogeous fungi. Canadian Journal of Forest Research 24:1516–1522.

WATERS, J. R., AND C. J. ZABEL. 1995. Northern flying squirrel densities in fir forests of northeastern California. Journal of Wildlife Management 59:858–866.

WELLS-GOSLING, N., AND L. R. HEANEY. 1984. *Glaucomys sabrinus*. Mammalian Species 229:1–8.

WHEATLEY, M. 2007. Fungi in the summer diets of northern flying squirrels (*Glaucomys sabrinus*) within managed forests of western Alberta, Canada. Northwest Science 81:265–273.

WHEATLEY, M., J. T. FISHER, K. LARSEN, J. LITKE, AND S. BOUTIN. 2005. Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: the northern flying squirrel in Alberta, Canada. Journal of Applied Ecology 42:577–586.

WHITE, R. E. 1983. A field guide to the beetles of North America. Houghton Mifflin, Boston, Massachusetts.

WHITE, R. E., AND D. J. BORROR. 1998. A field guide to the insects: America north of Mexico. 2nd revised ed. Houghton Mifflin, Boston, Massachusetts.

ZAR, J. H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall, Upper Saddle River, New Jersey.

Submitted 12 January 2009. Accepted 7 July 2009.

Associate Editor was John L. Koprowski.